

Poor horse traders: large mammals trade survival for reproduction during the process of feralization

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We investigated density dependence on the demographic parameters of a population of Camargue horses (*Equus caballus*), individually monitored and unmanaged for eight years. We also analysed the contributions of individual demographic parameters to changes in the population growth rates. The decrease in resources caused a loss of body condition. Adult male survival was not affected, but the survival of foals and adult females decreased with increasing density. Prime-aged females maintained high reproductive performance at high density, and their survival decreased. The higher survival of adult males compared with females at high density presumably results from higher investment in reproduction by mares. The high fecundity in prime-aged females, even when at high density, may result from artificial selection for high reproductive performance, which is known to have occurred in all the major domestic ungulates. Other studies suggest that feral ungulates including cattle and sheep, as these horses, respond differently from wild ungulates to increases in density, by trading adult survival for reproduction. As a consequence, populations of feral animals should oscillate more strongly than their wild counterparts, since they should be both more invasive (as they breed faster), and more sensitive to harsh environmental conditions (as the population growth rate of long-lived species is consistently more sensitive to a given proportional change in adult survival than to the same change in any other vital rate). If this principle proves to be general, it has important implications for management of populations of feral ungulates.

Keywords: population dynamics; density dependence; feralization; reproductive performance; ecosystem restoration; equid

1. INTRODUCTION

Understanding the processes driving variations in population growth, i.e. changes in population size from one year to the next, is the core of population ecology. This knowledge also is critically important for the management of populations, be they plants or animals. Large herbivores are particularly important as they play a central role in ecosystems (Danell *et al.* 2006): under favourable environmental conditions, their populations usually increase strongly before reaching high density, and thereby density dependence (Forsyth & Caley 2006). It is now well established that density-dependent responses of large wild herbivores follow a predictable pattern (Eberhardt 1977) involving a sequential response from juvenile survival to adult survival. Moreover, large herbivores have high adult survival rates that are resilient to environmental stresses (Gaillard & Yoccoz 2003 for a review). Domestic herbivores returning to the wild, called

feral hereafter, are increasingly important in ecosystem dynamics (e.g. Freeland 1990 for large herbivores in Australia), yet the principles underlying the density-dependent responses in feral populations have received little attention. Artificial selection has led to higher fecundity in domestic than in related wild species (Clutton-Brock 1981): it is therefore likely that the pattern of the density-dependent responses of feral populations will differ from that of wild species. However, though considerable data are available for wild species (Fowler 1987), little is known of the density-dependent responses in feral populations.

Two main approaches can be used to investigate density dependence in animal populations (Coulson *et al.* 2000; Krebs 2002): the pattern-oriented approach (or 'density paradigm') which allows biologists to identify direct or delayed effects of density on population growth rates from time series of population counts, and the process-oriented approach (or 'mechanistic paradigm') which is based on the decomposition of the observed variance in population growth into density-dependent and environmental variations of age-specific fecundities and survival rates. We used the second approach here because it makes it possible to discover how the performance of individual animals is influenced by the ecological context (e.g. food,

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Table 1. Criteria used for the visual condition index (from Duncan 1992).

condition class	criteria
excellent	'blocky' appearance, skeletal structures not perceptible
normal	ribs and pelvic bones covered
moderate	ribs perceptible, pelvic bones covered
thin	ribs visible not prominent, pelvic bones slightly covered
very thin	ribs and pelvic bones prominent
emaciated	ribs and pelvic bones project very prominently; abdomen often has a 'pinched' appearance; animal may be weak

predators, disease, climate, social stress). Perturbation analyses (*sensu* Caswell 2001) offer a powerful tool to investigate the principles underlying changes of population abundance with time: we use here the introduction of a population of large domestic herbivores into a natural environment as a 'field experiment' to discover whether domestic animals respond like wild ones (Sinclair 1989; Sinclair & Krebs 2002). We were able to examine the response of horses to a sharp increase in density from a long-term study of free-living feral horses (*Equus caballus*) in the Camargue (France) immediately after the cessation of management. Based on the principles discovered by Eberhardt (1977) for large wild mammals, we expected that the demographic traits of this feral population would respond to density in the following manner:

- (i) The number of horses would increase at the beginning of the study with a maximal population growth rate of approximately 30–35 per cent as expected in monotocous species (Gaillard *et al.* 2000) under favourable environmental conditions (abundant resources, no predation); the population growth rate would then show a density-dependent decline.
- (ii) A sequential reduction in foal survival, in reproductive performance of young females, and finally of prime-aged females would account for the decline in population growth.
- (iii) The survival of adult males would respond before that of females, as male–male aggression can cause increased male mortality (Berger 1983), and the adult sex-ratio in this species with weak sexual size dimorphism would be a little below 50 per cent males (as in mustangs, Feist & McCullough 1975).
- (iv) The demographic changes would be driven by declining body condition of the animals, driven by the depletion of food resources.

2. MATERIAL AND METHODS

(a) The population and the study area

The horses were of the Camargue breed and live on 330 ha in the delta of the River Rhône (Southern France). The initial herd was composed of 14 horses in 1974: yearlings (two males, two females), 2-year-olds (two males, one female), prime-aged male (5-year-old) and females (4-, 5-, 6-, 10-, and 13-year-olds) and one old female (19-year-old). The horses were not managed, except that 24 emaciated individuals (see table 1, category 6) whose life was considered at risk without special care were removed for ethical reasons in March 1981 and February–March 1982 (i.e. biological years

1980 and 1981); these are considered as dead in our analyses and consisted of foals (seven males, three females), yearlings (two males, one female) and adult females (ten 2–12-year-olds and one 19-year-old). The breeding females all had foals and had little chance of surviving without special care; nursing mothers in poor condition died in similar circumstances on a nearby estate. To prevent the sex ratio becoming strongly male biased, which does not occur in wild equids, nine males were removed in 1981: two yearlings, five 3-year-olds and two 4-year-olds. Finally to prevent damage to the range, the herd was reduced to approximately half of the maximum number in September 1982 (see Duncan 1992 for details). We therefore considered that the number of horses was manipulated only slightly in 1981 (11% of horses, all males, removed in the second part of the year) and investigated density-dependent effects on horse demography for eight years (1974–1981) when human management was negligible (table 2).

All the horses were individually known, and the population was monitored every day over the years 1974–1981, with the exception of most weekends; thus the dates of births and deaths were known exactly (the uncertainty around the date was never more than ± 1 day). During our study period, the birth sex ratio was unbiased (51% males, $n=113$, $\chi^2=0.11$, $p=0.74$) and did not change throughout the study period (logistic model: $n=8$, slope 0.0812 (\pm s.e. = 0.0907), $p=0.371$). The foaling rate was measured accurately (particular care was taken to check females in late pregnancy for blood on the hind legs if they were no longer visibly pregnant and not accompanied by a newborn foal). The timing of births was described from the foals born between 1974 and 1983: the median birth date was 14 April ($n=118$). Thirty-eight per cent of births occurred in April and mares foaled from November to August. To account for the long birthing period when assessing foal survival, we defined a cohort around a date close to the median birth date so that the biological year [t] lasted from 1 April [t] to 31 March [$t+1$].

For each breeding mare, a condition score was noted (table 1) by one observer, in the middle of each month from October 1978 to September 1983; photographs of each horse were used for 1975–1977. Here, we used the median condition score of breeding mares (i.e. females that had foaled at least once; see Monard *et al.* 1997) in March, a month before the beginning of each biological year. The body mass of breeding mares was also measured using a Maréchal balance in March each year from 1980 to 1983. Because the mean condition index was closely related to the mean body mass of mares (for horses > 350 kg: $\text{weight} = -24.93 \times \text{condition} + 467.84$; $n=7$, $p=0.0003$, $R^2=0.94$), we used the condition index only in these analyses.

Table 2. Data on climate, food, the condition status of mares, horse density and population growth rate between 1974 and 1981. (Notation is defined as follows: 'year' is the biological year; 'rain' is the annual rainfall (September–August); the winter food resources were measured as the quantity ('herb biomass') and quality ('CPh') of the herb layer in January, and the quality of the spring diet as the faecal crude protein in April ('CPF'); 'condition' is the mean body condition index of breeding mares at the end of the winter (March); N is the population size before foaling; r is the annual population growth rate.)

year	rain (mm)	winter food (quantity) 'herb biomass'	winter food (quality) 'CPh'	spring diet (quality) 'CPF'	condition	N	r
1974	936					14	0.31
1975	506	575		12.6	2	19	0.27
1976	628	515	6.4	11.4	2.2	25	0.31
1977	950	500	5.5	10.3	2.3	34	0.23
1978	816	485	7.6	9.6	2.4	43	0.26
1979	437	470	5.1	9	2.9	56	0.21
1980	777	365	6.1	10.2	3.3	69	0.10
1981	463	315	5.0	8.3	4.4	76	

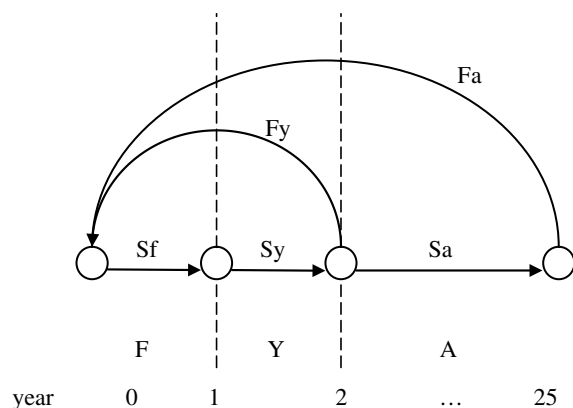


Figure 1. Life cycle of a Camargue mare: F=foal; Y=yearling; A=adult. Note that the adult stage can be further subdivided into young, prime-age and senescent stages. Straight lines indicate transitions from one stage to the next, and curved lines indicate reproduction. The life cycle is described by demographic rates: Sf=foal survival (annual survival during the first year of life); Sy=yearling survival (annual survival between 12 and 24 months); Sa=adult survival (annual survival of females older than 2 years); Fy=annual fecundity of yearling females; Fa=annual fecundity of adult females (≥ 2 year-olds).

The age at first foaling was 24 months (for 27 young breeding mares monitored between 1974 and 1982: 10 first reproduced as 2-year-olds, 16 as 3-year-olds, and 1 as a 4-year-old), and the maximal longevity was 25 years (figure 1). Females grew until they were 7-year-olds, and males until 6-year-olds (Duncan 1992, p. 156). The adult age class of ungulate species is usually divided into different stages: young, prime-aged and senescent adults (Gaillard *et al.* 2000). For these horses, we therefore analysed variations in demographic parameters (survival and fecundity) in testing different age structures in adult males and females (≥ 2 year-olds). The demographic data were coded as binary variables: '0' for 'dead' or 'no reproduction' and '1' for 'alive' or 'reproduction' during the biological year (for survival and fecundity, respectively). In this study, fecundity corresponds to the probability of giving birth to a full-term foal because litter size is one in horses. Annual survival and fecundity are age specific and were calculated from 1 April to 31 March of each year from 127 individual life histories monitored between 1974 and 1981. A cohort is defined as all individuals

born in the same biological year, and foals born between November [$t-1$] and 31 March [$t-1$] are included in the cohort of year [t].

Plant production in Mediterranean environments is limited by temperature in winter and soil humidity in summer: the rain in autumn and winter affects plant growth the following summer more strongly than in the calendar year, so annual rainfall (table 2) was calculated for each year from September [$t-1$] to August [t] as in Duncan (1992). For 9 years (1975–1983) the availability of food resources in the limiting season (winter) was measured quantitatively (herb layer biomass; table 2), and qualitatively (crude protein content of the herb layer; table 2). These measures came from samples of the vegetation clipped to ground level in 25×50 cm quadrants in each of six vegetation types in January of each year from 1975 to 1983 (see Duncan (1992) for details of the sampling methods). The faecal crude protein concentration (table 2) also was used as an index of the quality of the diets ingested by horses in the breeding season (April; see Mésochina *et al.* 1998 for a justification).

(b) Statistical analyses

Among the dependent variables, there was no correlation between either rainfall or crude protein content in winter and all other variables. However, horse density was closely linked to both herb biomass ($r = -0.955$; $p < 0.001$) and mares' condition index ($r = -0.956$; $p < 0.001$). Spring diet quality (faecal crude protein) was correlated to both horse density ($r = -0.835$; $p = 0.019$) and mares' condition ($r = -0.748$; $p = 0.044$). We therefore tested the effects of density (including nonlinear effects) on demographic parameters in combination with rainfall only.

The annual population growth rate is defined as $r = \ln(N_{t+1}/N_t)$ where N is the population size before foaling. We first tested for density dependence in r and then in survival and reproduction. We used logistic models to test the effects of density and other factors on horse survival and fecundity within different age- and sex classes during the period 1974–1981. As survival of adults generally differs between the sexes in ungulates (Toigo & Gaillard 2003) and as Camargue stallions and mares start breeding at 2 years of age (Duncan 1992; Feh 1999), we used separate analyses for the two sexes, for horses of 24 months and older. We first performed an analysis of age dependence on adult (≥ 2 -year-old) demographic parameters using logistic models, and the selected age-dependent model was then

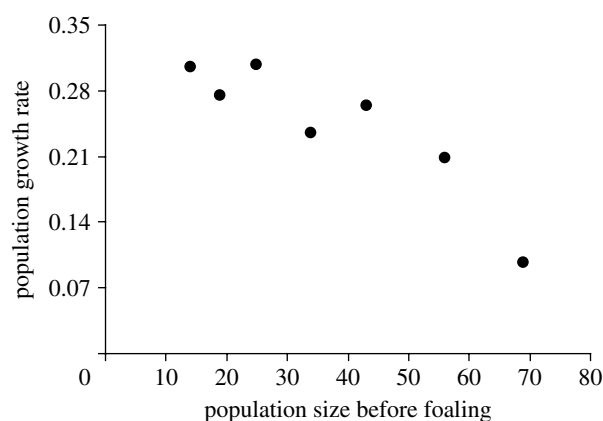


Figure 2. The effect of density on the annual population growth rate (1974–1981).

used to assess density and rainfall effects. Model selection was based on the Akaike Information Criterion corrected for small sample size (AICc; Burnham & Anderson 2002). We selected models with the lowest AICc; when competitive models were within 2 units of AICc scores, we selected the simplest model. We used the proportion of explained deviance as a measure of the explanatory power of our models (Crawley 2007).

Finally we performed an analysis to estimate individual contributions to the population growth rate using a de-living approach (Coulson *et al.* 2006). An individual's contribution represents the individual's realized annual fitness.

3. RESULTS

(a) Effect of density on the population growth rate

The population increased rapidly until 1979 (r of approx. 0.30), the growth rate then declined to 0.21 in 1979 and 0.10 in 1980 (table 2). There was therefore marked density dependence in population growth, and the linear model provided a satisfactory fit for the data ($r=0.362-0.003 \times N$; $n=7$; $p=0.006$; $R^2=0.81$), though there was a suggestion of nonlinearity indicated by a pronounced negative response to density increase above 20 horses per km^2 (i.e. a population size of 70 horses) in 1980 ($r=0.281+0.002 \times N-6.10^{-5} \times N^2$; $n=7$; $p=0.014$; $R^2=0.88$; figure 2), but the quadratic term was not significantly different from 0 ($-6.10^{-5} \pm 4.10^{-5}$; $t=-1.528$; $p=0.201$).

(b) Effect of density on the demographic parameters of the horses

(i) Survival rates

One hundred and thirteen foals were monitored between 1974 and 1981. The effects of interactions between horse density and sex (changes in slope of -0.079 ± 0.051 ; $p=0.119$, males used as a reference) and between horse density and rainfall (slope of the product between density and rainfall of 0.010 ± 0.765 ; $p=0.990$) were not retained in the final model. There was no influence of either sex (slope of -0.488 ± 0.472 ; $p=0.301$, males used as a reference) or annual rainfall (slope of 0.002 ± 0.001 ; $p=0.103$) on foal survival in these years, but the increase of horse density had a strong negative influence (slope of -0.068 ± 0.019 ; $p<0.001$; table A in appendix in the electronic supplementary materials; figure 3).

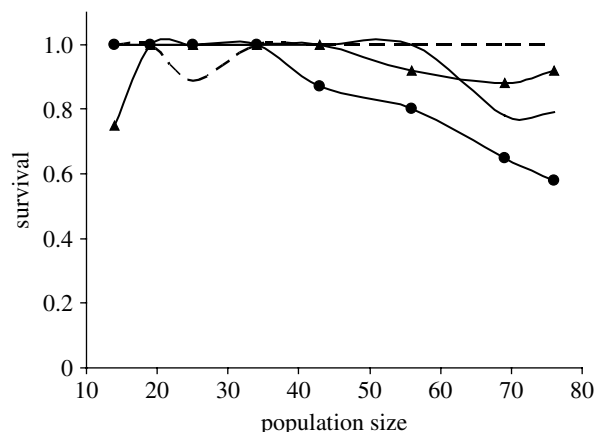


Figure 3. The effect of density on the annual survival of Camargue horses (1974–1981). Circles, foals; up-triangles, yearlings; dashed line, males older than 2 years; solid line, females older than 2 years.

The selected model included horse density only, and accounted for 17.4 per cent of the observed variations in foal survival.

Seventy-seven yearlings were monitored between 1974 and 1981. Although there was no significant main effect of horse density (slope of -0.018 ± 0.024 ; $p=0.462$), density dependence may have occurred (figure 3). The low point in 1974 is caused by the death of one of the four yearlings in the population, which died when foaling (figure 3). Rainfall (slope of $-4.10-4 \pm 0.002$; $p=0.874$) and sex (slope of 0.461 ± 0.943 ; $p=0.625$), and interactions among these factors did not have significant effects on yearling survival. The best model corresponded to a high and constant survival over time (0.93 ± 0.09 ; table B in the appendix of the electronic supplementary material).

Only one male, a 4-year-old in 1976, died during the eight years. As a consequence, the best model corresponded to a high and constant survival of adult males over time (0.99 ± 0.04 ; figure 3).

The model including full age dependence (i.e. including age as a discrete factor) for the survival of thirty-six adult females (≥ 2 years old) did not show a clear age structure. The slopes differed between the first age ('2-year-old', used as a reference) and '7-year-old' (slope of -1.723 ± 1.112 ; $p=0.121$), '11-year-old' (slope of -1.540 ± 1.367 ; $p=0.260$) and '17-year-old' (slope of -2.639 ± 1.592 ; $p=0.097$). We therefore tested models with different age structures (see legend in table C in the appendix of the electronic supplementary material). There was no effect of rain (slope of 0.002 ± 0.002 ; $p=0.271$) on the annual survival of adult females between 1974 and 1981. The best model accounted for 32.2 per cent of the total deviance and included two age classes (2–16-year old and ≥ 17 -year old) and a linear effect of density (slope of -0.149 ± 0.053 ; $p=0.005$; table C in the appendix of the electronic supplementary material; figure 3). The effects of density differed between these two age classes during our study period, with a decline in the survival of 2–16-year-old mares from 1 for 1974–1979 to 0.82 in 1981. The three oldest mares (≥ 17 -year old) died successively in 1979, 1980 and 1981, leading to a sharp decline in survival from an average of 0.88 for 1974–1979 to 0 in 1980–1981.

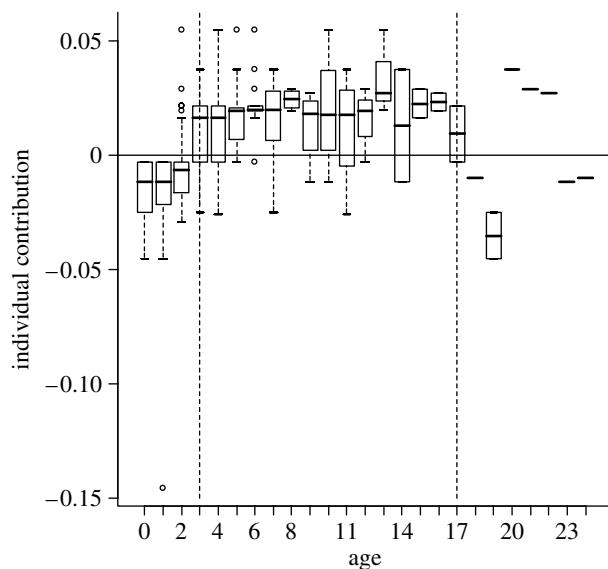


Figure 4. Variations of female individual contributions with age.

(ii) Female fecundity

Yearling females mated in the first years of the study except 1976, which was considered to be due to incest avoidance, rather than because they were not developed enough to ovulate (Duncan 1992, p. 158): the fecundity of 2-year-old females in 1977 was therefore considered as missing data. The model including full age dependence for the fecundity of 37 adult females (≥ 2 year-old) showed a clear age structure with changes in slopes between the first age ('2-year-olds', used as a reference) and the following ages: from 3 to 6 year-olds (slopes between 2.033 ± 0.742 and 2.949 ± 1.109 ; $p < 0.015$), 7 to 18 year-olds (slopes of 19.807 ; $p > 0.996$) and > 18 year-olds (slope of 0.241 ± 1.471 ; $p = 0.870$). We therefore tested models with different age structures (see legend in table D in the appendix of the electronic supplementary material). The best model included four age classes and accounted for 29.4 per cent of the total deviance. Female fecundity was $0.44 (\pm 0.51)$ for 2-year-olds, $0.90 (\pm 0.31)$ for 3–6 year-olds, 1 for 7–18 year-olds, and $0.71 (\pm 0.49)$ for females older than 18 years. There was no significant effect of rain (slope of 0.001 ± 0.001 ; $p = 0.453$) or density (slope of -0.012 ± 0.012 ; $p = 0.304$) on the fecundity of breeding mares between 1974 and 1981 (table D in the appendix of the electronic supplementary material). The age at first reproduction did not vary significantly among cohorts (ANOVA: $F_{7,17} = 1.356$; $p = 0.285$).

(iii) De-lifing analysis

We performed a de-lifing analysis on 62 females monitored between 1974 and 1981, analysing individual contributions for survival and recruitment (i.e. whether a female raises a foal to 1 year of age or not, in a given year). There was a clear age structure with, not surprisingly, markedly age-specific contributions with the prime-aged contributing much more than younger and older females (-0.014 ± 0.019 for juvenile females [0–2 year-olds], 0.016 ± 0.017 for prime-aged females [3–17 year-olds] and -0.001 ± 0.029 for old females [≥ 18 year-olds], $F_{2,230} = 70.513$; $p < 0.001$, figure 4). We therefore analysed the patterns of juvenile and prime-aged females in relation to density.

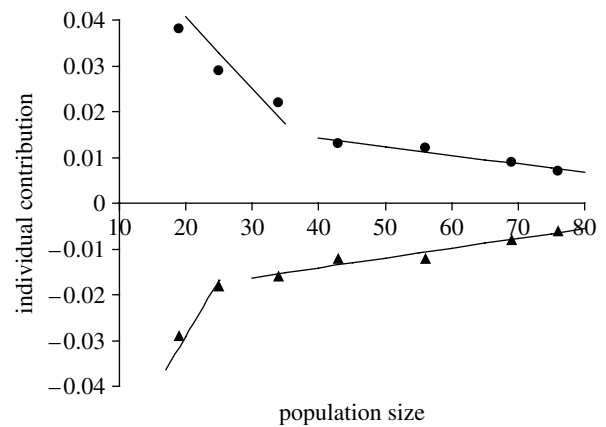


Figure 5. The effect of density on the annual individual contributions of Camargue females. Triangles, juvenile females; circles, prime-aged females.

The relative annual individual contributions of juvenile females increased strongly with density when the population size was below 30 horses, then slightly increased after this threshold ($IC = -0.0777 + 0.0024 \times N$ if $N < 30$ and $IC = -0.0893 + 0.0024 \times N + 0.0022 \times (N - 30)$ if $N > 30$, $p = 0.0003$, $R^2 = 0.99$; figure 5). In contrast, the relative annual individual contributions of prime-aged females decreased strongly when the population size was below 40 horses, then slightly decreased after this threshold ($IC = 0.0720 - 0.0016 \times N$ if $N < 40$ and $IC = 0.0766 - 0.0016 \times N + 0.0014 \times (N - 40)$ if $N > 40$, $p = 0.0023$, $R^2 = 0.96$; figure 5).

(c) Consequences of variations in the body condition of breeding mares

The condition of adult females at the end of winter, measured by the median condition index of breeding mares in March, was initially good (condition class 2.0, 'normal condition'). It declined slightly until 1979 and then fell sharply to 4.4 in 1981 (between thin and very thin; see table 2). The condition was closely and negatively correlated with the increase in density ($r_{\text{Pearson}} = 0.93$, $n = 7$, $p = 0.003$).

The abundance of the horses' food resources in winter ('herb biomass') declined by nearly a half over the 8 years (table 2), and the quality of their diet in the breeding season (measured by an index of dietary crude protein, 'CPf' in table 2) declined by about a quarter. The condition index of the mares was closely correlated with the abundance of the herb layer ($r_{\text{Pearson}} = -0.96$, $n = 7$, $p < 0.001$; note that animals in the best condition have the smallest value of this particular index, see table 1), and more weakly correlated with the quality of their diet (CPf) in the breeding season ($r_{\text{Pearson}} = -0.75$, $n = 7$, $p = 0.044$). There was no correlation between the mares' condition and the quality of the herb layer in winter ($r_{\text{Pearson}} = -0.55$, $n = 7$, $p = 0.262$). These results suggest that the process driving the decline in condition was depletion of the resources in both seasons, caused by the increase in density.

4. DISCUSSION

The rate of increase of the population after release was high (31% in the first year) as expected, and averaged 27 per cent in the period 1974–1979. After 1979, the population growth rate declined markedly with density.

Table 3. Comparison between demographic parameters (mean values) derived from Przewalski horses (Tatin *et al.* 2009; C. Feh 2007, personal communication), feral horses in the Great Basin (Berger 1986), Pryor Mountains (Garrott & Taylor 1990) and Kaimanawa (Cameron *et al.* 2001; Linklater *et al.* 2004), the Camargue horses studied at (this study) low and (this study) high densities and Cumberland Island at carrying capacity (Goodloe *et al.* 2000). (Populations were classed as at or close to carrying capacity when density dependence in *r* or reproductive success was demonstrated. All these populations were monitored on an individual basis for survival and/or reproduction.)

	Przewalski (Tatin <i>et al.</i> 2009; C. Feh 2007, personal communication)	Great Basin (Berger 1986)	Pryor Mountain (Garrott & Taylor 1990)	Kaimanawa (Cameron <i>et al.</i> 2001; Linklater <i>et al.</i> 2004)	Camargue (this study)	Camargue (this study)	Cumberland (Goodloe <i>et al.</i> 2000)
years	1994–2003	1979–1983	1977–1986	1994–1998	1974–1979	1980–1981	1986–1990
time (years)	10	5	10	5	6	2	5
population size	13–55	58–149	86–181	413	14–56	69–76	186–220
growth rate (<i>r</i>)	0.169	0.188	0.113	0.092	0.277	0.150	0.043
adult sex ratio	50	43	34 ^a	48	39	49 ^a	63
(% males)							
adult male survival	0.90–1	0.95	0.96	0.97	0.98	1	
adult female survival	0.90–1	0.95	0.99	0.94	1	0.79	0.92
foal survival	0.81	0.92	0.94	0.83	0.95	0.62	0.6
foaling rate (mares ≥ 3 years-old)	0.6–0.8	0.9	0.55 ^b	0.61	0.92	0.93	0.66
age at first reproduction (years)	3	3	3	3	2	2	3
population at or close to carrying capacity	yes (space-limited)	no	yes (but horses were removed)	yes (resource-limited)	no	yes (resource-limited)	yes (resource-limited)

^a Sex ratio biased as a consequence of management.

^b Underestimate.

These results are therefore in agreement with previous studies on large mammals: the rate of population growth declines at high densities (Fowler 1981). At low densities, the rate of increase in these horses is high compared with other equids (table 3). This difference between the Camargue horses at low density and the others is likely to result from earlier, and/or higher rates of, reproduction (see table 3, 'age at first reproduction' and 'foaling rate').

Our second expectation was that the decline in the population growth rate, as observed in wild ungulates, would be caused first by a reduction in foal survival and in reproductive performance and last by the survival of adult females. Foal survival did indeed decline strongly as density increased from 5 to 23 horses km⁻². Fecundity was strongly age-structured in these horses, as in wild ungulates, and the fecundity of young females declined at high density (see Duncan 1992), though not significantly in the years up to 1981. The fecundity of young mares in Przewalski's horses (*Equus przewalskii*) was also density dependent, with a delayed age at first reproduction (Tatin *et al.* 2009). By contrast with wild herbivores, fecundity in prime-aged Camargue females remained high and quasi-constant at high density. Fecundity is an important criterion for horse breeders in the Camargue (P. Duncan 1979, personal observation), and it is possible that mares of this breed have been selected based on this criterion for a long time. Interestingly, a very similar pattern was reported from the intensive research on Soay sheep (*Ovis aries*; see fig. 3.5(d) p. 59, Clutton-Brock & Pemberton 2004). More generally, artificial selection for fecundity in domestic animals before release is the likeliest explanation for these differences between wild and feral herbivores: an earlier age at first reproduction has been found in other feral herbivores (e.g. Garel *et al.* 2005, for mouflon originated from crossing wild and domestic sheep). Likewise, in Soay sheep, parturition at 1 year of age and twinning rates of approximately 10 per cent are much higher than those in wild sheep (Clutton-Brock & Pemberton 2004; see Clutton-Brock 1981 for a general treatment).

The survival of adult males was not affected by density in this period. Yearling survival declined at high density but not significantly during our study period. As in other ungulates (e.g. Toïgo *et al.* 2007 for ibex, *Capra ibex ibex*), horses exhibit rapid growth during their first year, then it slows down during their second year (Duncan 1992, fig. 4 p. 156). Moreover, few yearlings (of either sex) breed, so they have lower energy requirements than foals and adults and may be more resistant to a decrease in the food supply for this reason.

Except for one 4-year-old, which died by accident in 1976, no other stallions died, or were even severely wounded. As the oldest stallion was only 12 years old in 1981, and as senescence has been estimated to occur after 15 years in feral horses (Garrott & Taylor 1990), this dataset is clearly unsuitable for the study of senescence in males. In other populations, stallion survival was also high but lower than in this herd, and male-male competition increased mortality (Berger 1983). The remarkably high survival in this study suggests that these Camargue stallions, when they reached adult weight, did not have important costs above maintenance.

The presence of females of a wide range of ages allowed us to show that the survival of adult females (≥ 2 year-old)

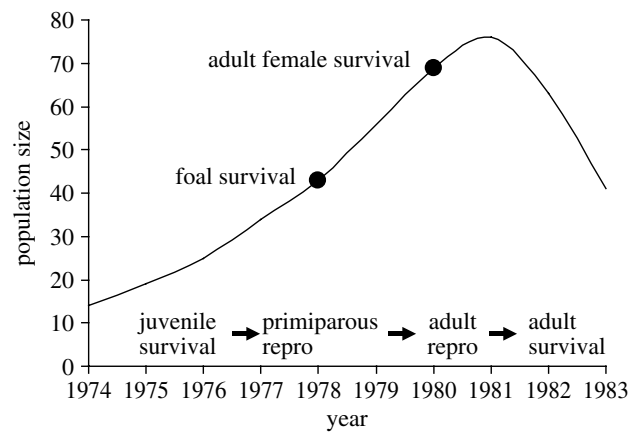


Figure 6. The sequence of density-dependent reactions of Camargue horses compared with the expectations based on Eberhardt's model and subsequent work (see §1).

was age-structured (2–16-year-old and ≥ 17 -year-old). By contrast with our third expectation, the survival of adult females decreased with density during our study period. Prime-aged survival (2–16-year-old) declined from 1 in 1974–1979 to 0.81 in 1980–1981 when density reached its highest levels. The mares lost body condition when density increased, and this loss was closely correlated with a decline of nearly 50 per cent in the horses' winter food supply (and with a decline in the quality of the diet in the breeding season). The survival of breeding mares therefore declined with age and condition, in response to increased intraspecific competition through depletion of the food resources. Five of the emaciated adult females did not actually die, but were removed in February–March 1982 (i.e. biological year '1981'). Had one or two survived, it would make some difference to the estimated adult female survival (0.79 without including these females versus 0.83 or 0.86). However the conclusion that adult female survival declined still holds.

These adult female horses traded off survival for reproduction: such a trade-off is expected to occur, according to evolutionary theory, but only in old animals (e.g. Williams 1957; the genetic basis of such a trade-off has been reported recently for wild ungulates, Wilson *et al.* 2007). Wild ungulates trade reproduction for survival during the prime-age stage ('selfish mothers' *sensu* Festa-Bianchet & Jorgenson 1998). These feral horses, in contrast, put their survival at risk when resources are limited. Reproductive costs in terms of survival reported in Soay sheep (Tavecchia *et al.* 2005) under harsh winters suggest that this could be a general phenomenon in feral populations of ungulates.

Young and prime-aged females contributed differentially to changes in population growth. Prime-aged females were more sensitive to density increases compared with young females, by contrast with what has been reported in other large herbivores (Gaillard *et al.* 2000). Moreover, the survival of prime-aged females and of their offspring, rather than their fecundity, accounted for the decline in the rate of population growth at high density, as fecundity of prime-aged females remained high until the end of the 8 years analysed here.

The density-dependent patterns we report differ strongly from the sequential Eberhardt model (1977), which is supported by most studies of wild large herbivores

(Gaillard *et al.* 2000). While foal survival declined first (in 1978) as expected by the model, the survival of prime-aged females (2–16 year-olds) declined with density (in 1980), although their reproductive rate was unaffected (figure 6), and the survival of prime-aged males was completely unaffected.

This study of Camargue horses is one of only two demographic studies of large herbivores released from domestication which are based on individual monitoring, and provide detailed information on both reproduction and survival as well as on the variations in the resources available (Clutton-Brock & Pemberton 2004 for Soay sheep). The survival of these Camargue horses varied with age and sex over the eight years, and we identified the demographic parameters that were affected by density, using a mechanistic approach. We showed that the density of the population influenced the food resources in terms of quantity as well as quality, and in spring as well as in winter. The increase in density was correlated with a loss of body mass and body condition in the mares, indicating that food limitation, exacerbated by intraspecific competition, was the process limiting this population (*sensu* White 2007). A previous analysis showed that the total production of this herd increased for six years (until 1979, 16.7 horses km⁻²) and then decreased to almost zero in 1982 (Duncan 1992, fig. 6 p. 18). Our fourth expectation, that density dependence in population growth is mediated through declining body condition, is therefore fulfilled.

There were clearly two different periods in this study: 1974–1979 when food was not limiting, and 1980–1981 when it was limiting, and density-dependent responses mainly on survival caused the population growth to decrease. Comparison of the recently released Camargue horses with feral and wild horses (table 3) allows some general principles to be identified. When food is not limited, horses have high survival at all ages in both feral and wild populations; the foaling rate of some of the feral populations (the Camargue and the Great Basin horses) is higher than that of wild horses. When food is limiting, Camargue mares trade survival for reproduction. Cumberland Island mares may also do so: their survival was lower compared with other feral mares even though they produced fewer foals, and the sex ratio became male biased. The differences in adult survival between males and females of the Camargue herd also led to a male-biased sex ratio: males over 2 years old represented 30 per cent of adults in 1974 and they reached more than 60 per cent in 1982 (Duncan 1992). Most feral horse populations have female-biased sex ratios (see Linklater 2000 and Linklater *et al.* 2004 for reviews), but the other studies where the population was resource-limited had male-biased adult sex ratios as those in the Camargue: on Sable Island (Welsh 1975) and Cumberland Island (Goodloe *et al.* 2000). Male-biased sex ratios have also been found in feral populations of other feral ungulates, cattle (Berteaux & Micol 1992) and sheep (Réale 1996), supporting the suggestion that this general principle may be true for all these species of ungulates. The between-sex differences reported in populations of wild large herbivores are quite different: males suffer relatively more than females from adverse conditions such as high density or harsh climate (Toïgo & Gaillard 2003), leading to female-biased sex ratios among adults (Berger & Gompper 1999).

In conclusion, this study shows that though feral horses rapidly return to a wild-type social system with harems and bachelor groups (Duncan 1992), their demographic responses to density differ from those of wild horse populations. This may result from selection for high reproductive output, which is known to have occurred in domestic herbivores (Clutton-Brock 1981). Such artificial selection leads not only to different responses to density, but also to earlier senescence of demographic parameters (see Mysterud *et al.* 2002 for an example on reproductive senescence in domestic sheep). As a consequence, the dynamics of feral populations may be profoundly different from that of their wild counterparts: the high reproductive rates of the feral ones will give them a greater potential to be invasive; but their maladaptive trade-off of survival against reproduction may make the feral populations more vulnerable to adverse environmental conditions (e.g. harsh climate, food limitation). Introduced feral populations may therefore oscillate more strongly and need more management, whether this is to prevent them from invading or to maintain them in difficult conditions when they are used as surrogates for extinct wild species, for instance in 're-wilding' programmes (Vera 2006). It is conceivable that the use of feral animals, less well adapted to the wild, may pose ethical problems, as well as ecological and behavioural ones, in such re-wilding programmes.

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